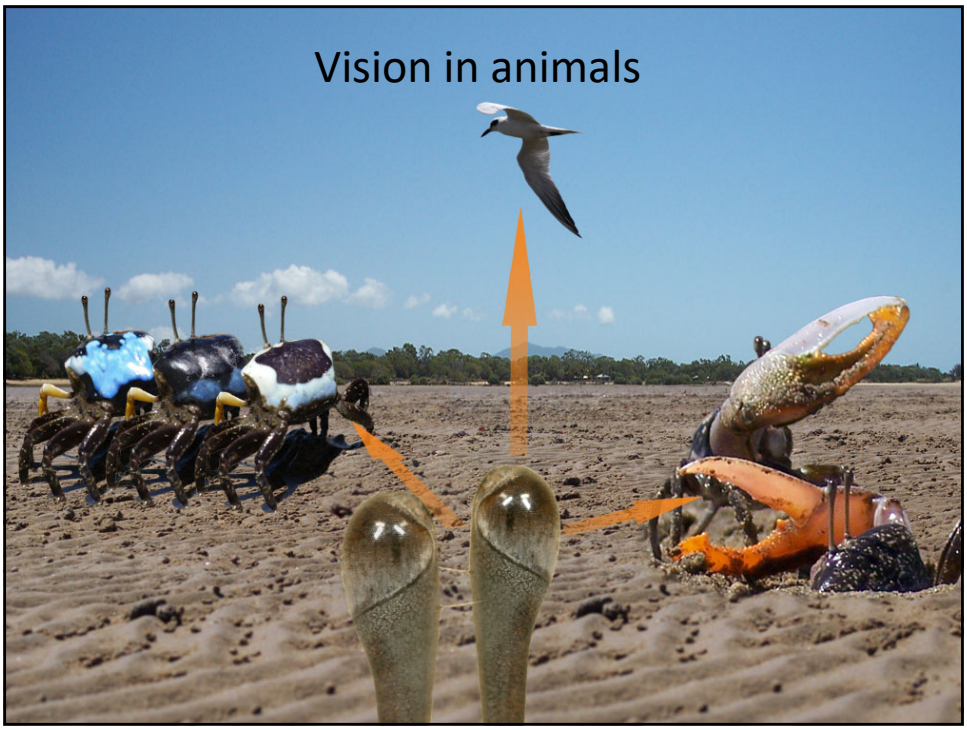
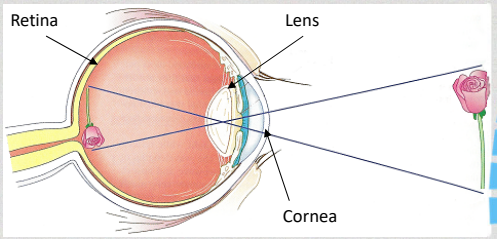
Vision in animals



1

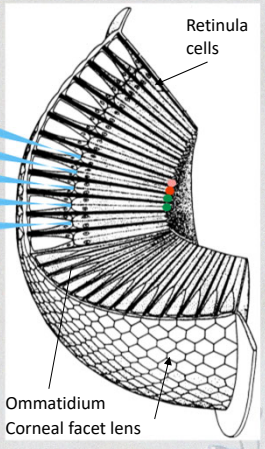
What makes eyes work? Visual ecology

A lens eye



Lens eyes:
Vertebrates
Molluscs
Spiders

A compound eye



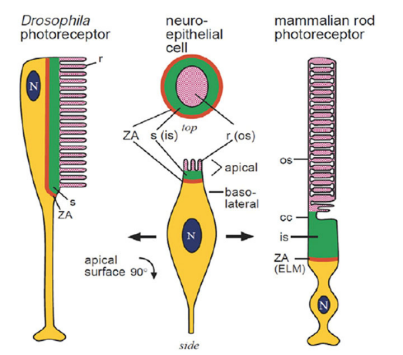
Compound eyes:
Insects
Crustaceans
Polychaete Worms

After Beatty 1995; Wehner 1981

2

Cilia vs microvilli

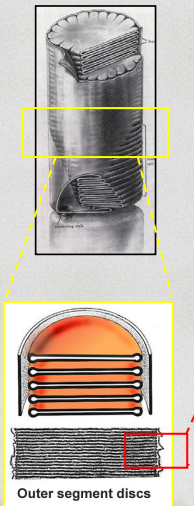
- Modern eyes evolved independently many times over the last 530+ Myrs Photoreceptor cells & visual pigments predate eyes and are less varied
- **Ciliary photoreceptors:** membrane expansion based on extension of cilium; Hyperpolarize with light
- **Rhabdomeric photoreceptors**: membrane expansion based on organisation of regular microvilli; Depolarize with light



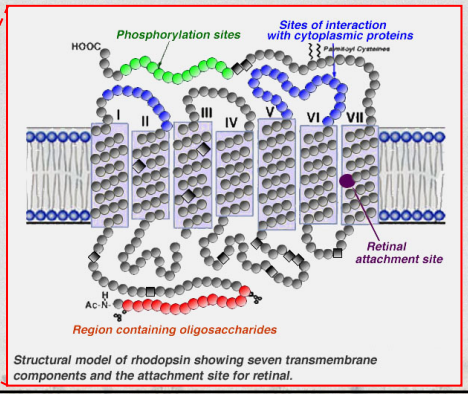
From Ready & Tepass 2004

3

Visual pigments: start of the photo-transduction cascade

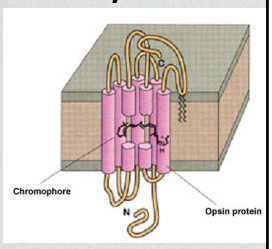


- Visual pigment = Opsin protein + chromophore
- Embedded in disc membranes
- Opsin proteins consisting of ca. 350 amino acids
- 7 transmembrane helices



4

Visual pigments: spectral sensitivity



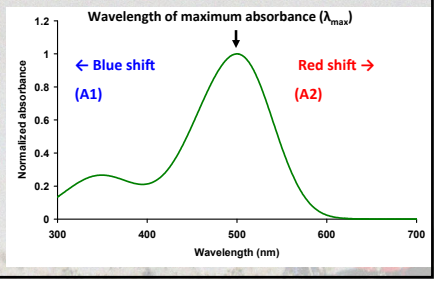
Spectral tuning is achieved by opsin modifications and selection of chromophore

Vertebrates - 2 chromophore types:

- 11-cis retinal (aldehyde of vitamin A1)
- 3,4-didehydroretinal (aldehyde of vitamin A2)

A1 “rhodopsins”: blue shifted sensitivity

A2 “porphyropsins”: red shifted sensitivity

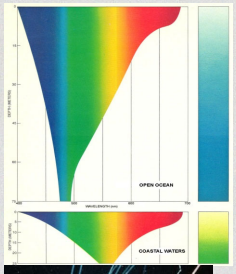


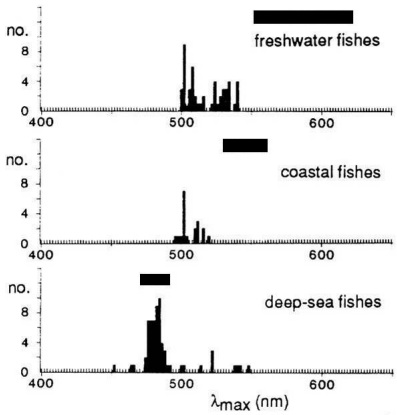
Rhodopins - terrestrial and marine

Porphyropsins - estuarine / freshwater

5

Spectral tuning



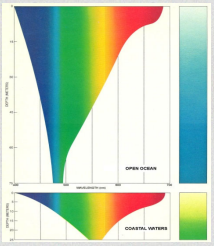


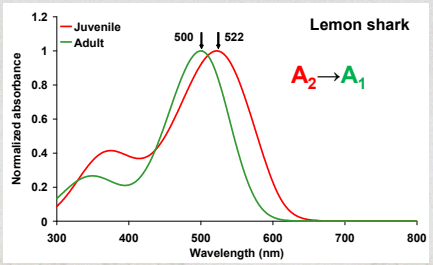
Histograms of λ_{max} values of rod visual pigments measured by microspectrophotometry of fishes from three habitats. The horizontal bars indicate the possible range of visual pigments most likely to confer maximum sensitivity in the different water types (after Lythgoe, 1988). Only the deep-sea fishes have rods best positioned to maximize photon catch. (Data mainly from Partridge *et al.*, 1988, 1989; Levine & MacNichol, 1979; Loew & Lythgoe, 1978.) (Figure from Partridge, 1990)

6

Ontogenetic variation

Elasmobranch

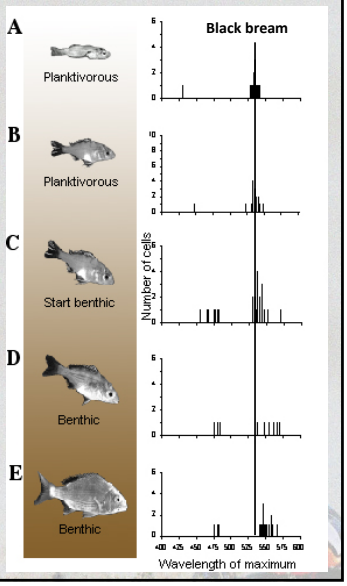




← Chromophore shift

Opsin shift →

Teleost



7

Colour vision?

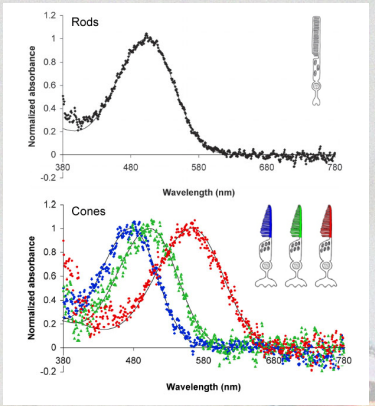
Requires:

- Two or more spectrally distinct photoreceptors
- Neural circuitry to compare outputs (i.e. colour opponency)

Types:

- Monochromacy – (no colour vision) , sharks, marine mammals
- Dichromacy - e.g. reef fish, crustaceans
- Trichromacy - e.g. rays
- Tetrachromacy - e.g. turtles, birds

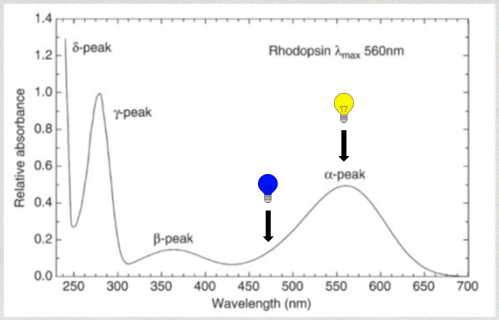
Stomatopods = 12-16!



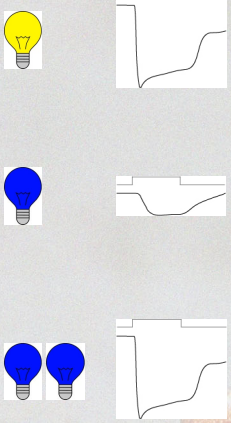
Hart et al 2004

8

The principal of univariance



Stimulus Response



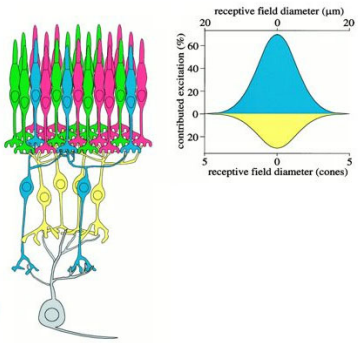
"The output of a receptor depends upon its quantum catch, but not upon what quanta are caught."

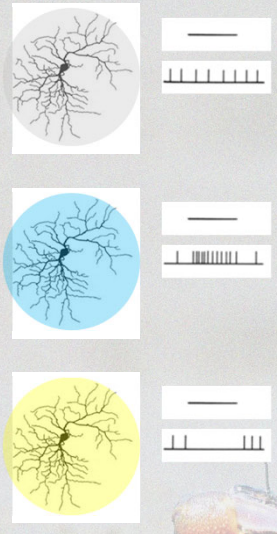
...Colour vision requires the comparison of cone types

9

Colour opponency

Blue/yellow pathway





Blue cone ON-bipolar

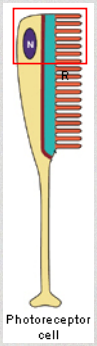
Diffuse (red + green) cone OFF-bipolar

Colour vision requires the comparison of cone types

http://www.cns.nyu.edu/~david/courses/perception/lecturenotes/color/color.html

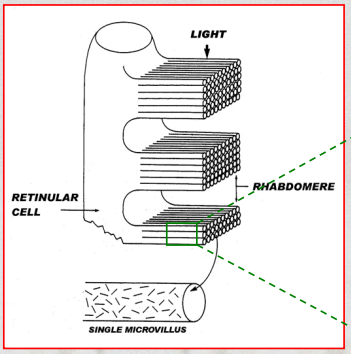
10

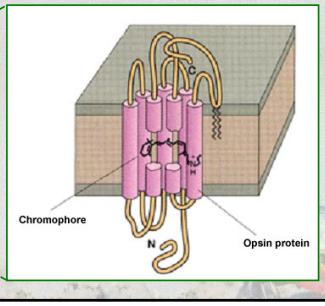
Visual pigments in rhadomeric PR



Visual pigment = Opsin protein + chromophore

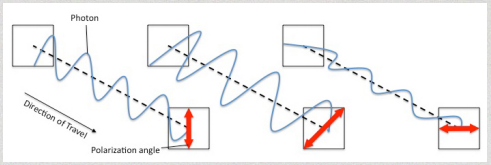
Like for ciliary PR, they are embedded in membrane, but the organisation is different



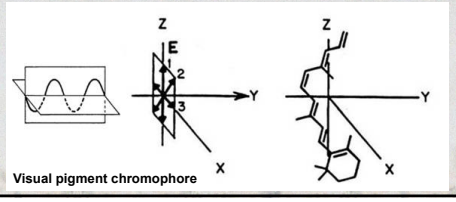


11

Polarization vision



Visual pigment chromophores preferentially absorb light polarized parallel to their long axis (Z-axis)

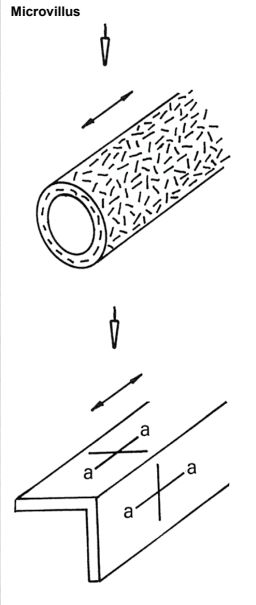


- Polarization sensitivity (PS) is found in many invertebrates:
  - insects
  - crustaceans
  - cephalopods
- Polarization has numerous uses:
  - Species recognition
  - Prey detection
  - Navigation / orientation

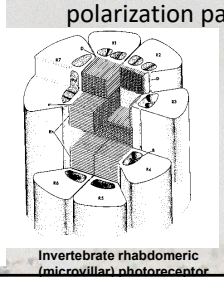
Also found in some vertebrates, e.g fish, but mechanism unclear

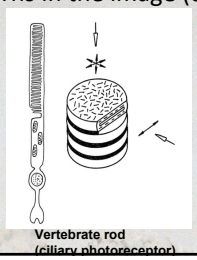
12

Polarization vision



- The geometry of the microvilli (long tubes) means that chromophores have a 2:1 bias of being aligned parallel to the microvilli long axis (a-a direction)
- Thus, microvilli preferentially absorb light that is polarized parallel to their long axis → individual photoreceptor cells are inherently polarisation sensitive
- Signals from photoreceptors with orthogonal rhabdomeres can be compared to discriminate polarization patterns in the image (cf. colour)


Invertebrate rhabdomeric (microvillar) photoreceptor


Vertebrate rod (ciliary photoreceptor)

13

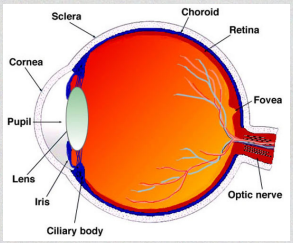
Focussing: terrestrial vs aquatic eyes

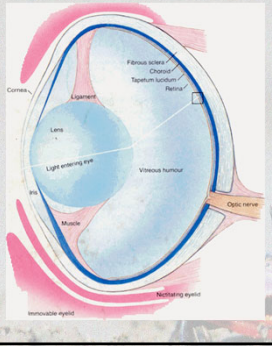
Terrestrial eyes

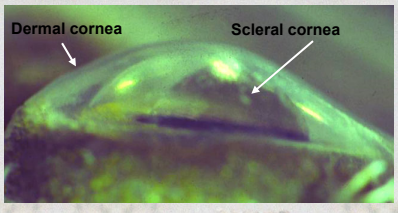
- Cornea is the major refractive element
  → highly curved cornea; thin, elastic lens

Aquatic eyes

- Cornea has no optical power
  → flattened cornea; near spherical



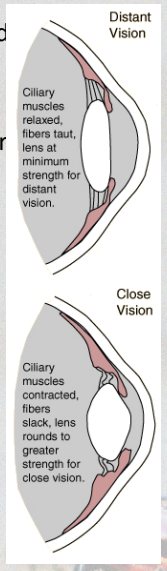


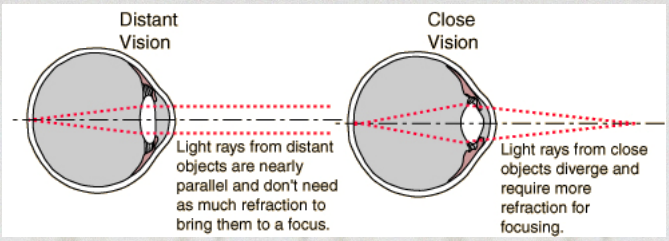


14

Accommodation - terrestrial eyes

- Snakes - increased pressure in the vitreous humour generated muscles near the iris pushes the lens forward
- Reptiles, birds and mammals - curvature of elastic lens is alter ciliary muscles


Distant Vision
Ciliary muscles relaxed, fibers taut, lens at minimum strength for distant vision.
Close Vision
Ciliary muscles contracted, fibers slack, lens rounds to greater strength for close vision.

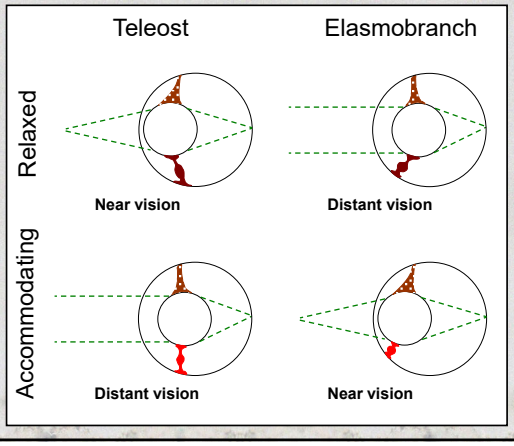

Distant Vision
Close Vision
Light rays from distant objects are nearly parallel and don't need as much refraction to bring them to a focus.
Light rays from close objects diverge and require more refraction for focusing.

15

Accommodation - aquatic eyes

- Teleosts (bony fish) - Retractor lentis muscle attached to lens moves lens backwards for distant vision

Cartilaginous fish - Protractor lentis muscle attached to lens pulls the lens forward for near vision

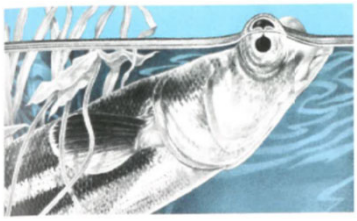


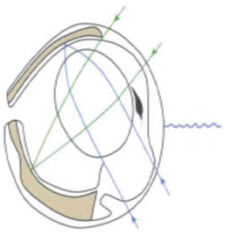
16

When you have to look in both places at once!

The four eyed fish *Anableps dowi*

Above water lens needs to do less work because of the contribution of the cornea, so the lens is thinner





17

Simple eyes with mirror optics

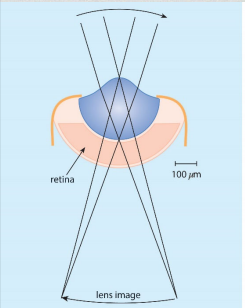


Figure 2. Path of rays refracted on the lens. Using the lens only, one would get an image far behind the retina.

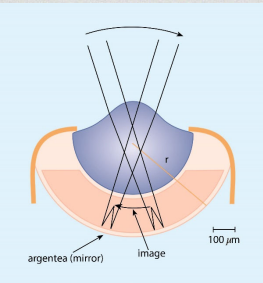
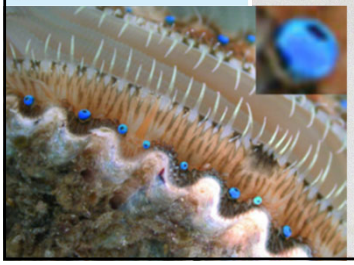


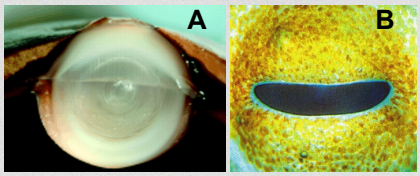
Figure 3. The image on the retina is mainly formed by reflection.

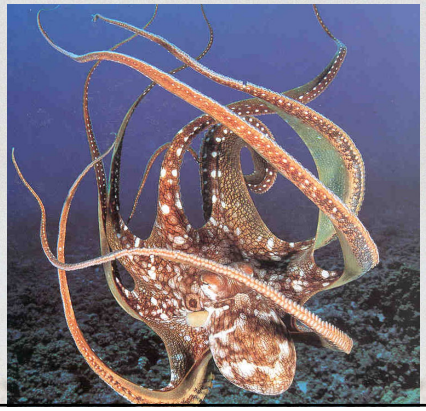


- Weak gelatinous lens
- Concave mirror at back of eye produces image at level of retina
- Focal length equal to half the radius of curvature (if spherical)
- Different from a tapetum
- Found in scallops of genus Pecten

18

Spherical lenses - octopus, squid





- Cephalopods such as octopus and squid have spherical lens (A) eyes similar to other aquatic vertebrates
- No cornea - anterior of eye is open to the sea water
- Lens moves back and fore like in fish
- Round pupil closes to horizontal slit (B) in bright light
- Good resolution (6 cycles/deg)

19

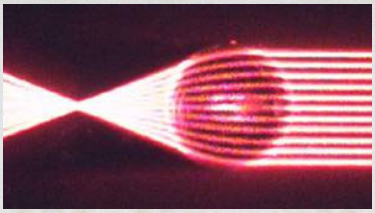
Lens design - spherical aberration

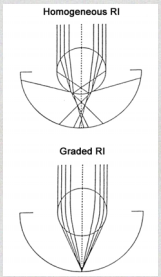
All lenses of uniform refractive index (RI) suffer from spherical aberration (like all our man-made lenses)

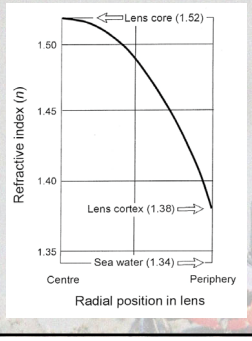
Becomes worse with increasing lens size and sphericity

Corrected with refractive index gradient

- Centre of lens - high RI
- Periphery - lower RI





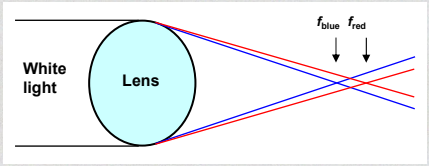


20

Lens design - chromatic aberration

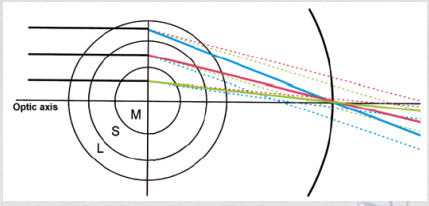
Lenses of uniform refractive index also suffer from longitudinal chromatic aberration

Left uncorrected, light of different wavelengths would have different focal planes in the retina



Fish and other vertebrates have evolved lenses with multiple focal lengths

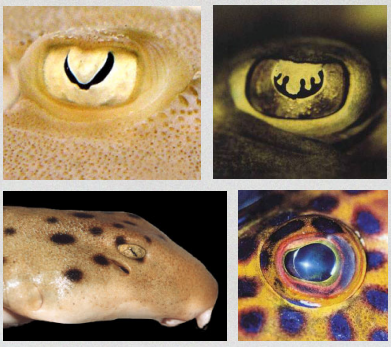
Different zones of the lens have different focal lengths that serve to focus different wavelengths of light to the same plane



21

Pupil

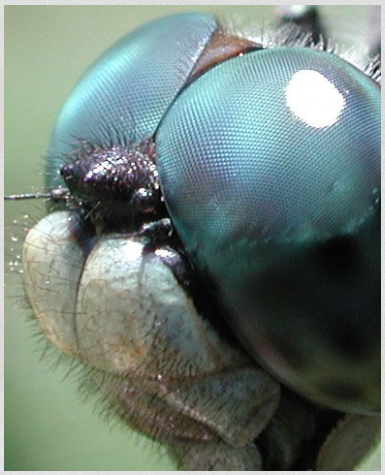
- Controls amount of light entering eye
- Affects spatial frequencies reaching retina in different planes
- Determines diffraction limit to resolution
- Trade off between large pupil for diffraction limited vision and good light capture vs. blurring due to optical aberrations



22

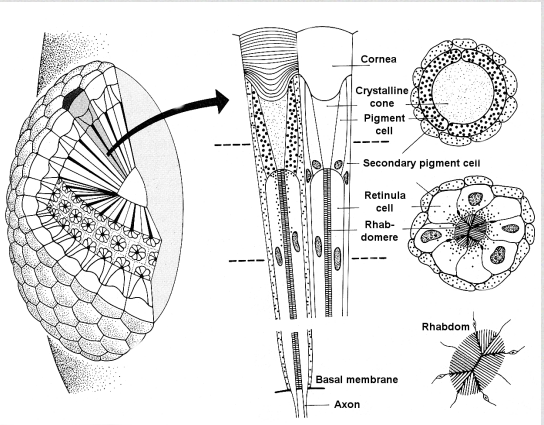
Compound eye types

- Apposition
- Optical Superposition:
  - Refracting superposition
  - Reflecting superposition
  - Parabolic superposition
- Neural Superposition



23

Apposition compound eyes

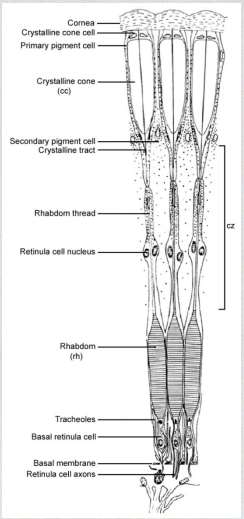


- Crystalline cone acts as light guide & scrambles image
- Rhabdoms in adjacent ommatidia optically isolated by a layer of opaque pigment
- Final 'image' is pixelated and upright/erect
- Found in most diurnal insects, e.g. bees, flies, butterflies, also horseshoe crabs (*Limulus*), amphipods (*Phronima*) and some crustaceans (fiddler crabs)

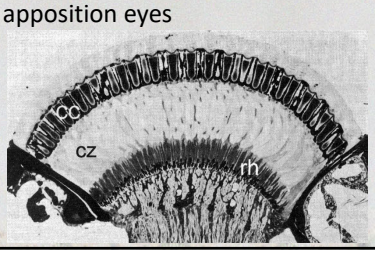
Wehner&Gehring (1990) Zoologie

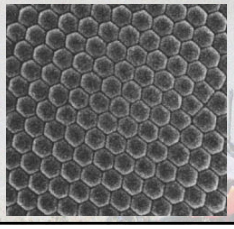
24

Optical superposition eyes



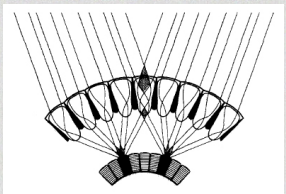
- Superposition eyes produce a single, deep-lying, erect image directly on the retina
- Crystalline cones (cc) separated from visual pigment-containing rhabdoms (rh) by a wide, optically transparent 'clear zone' (cz)
- Clear zone allows light rays from several adjacent crystalline cones to reach a single rhabdom
- Refracting superposition eye has high sensitivity (ca. ×100 greater than apposition eye of same size)
- Resolution can be as good as for similarly sized apposition eyes



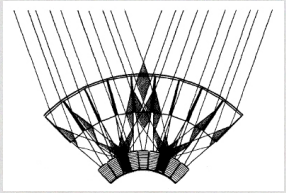


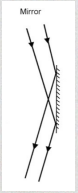
25

Optical superposition eye types

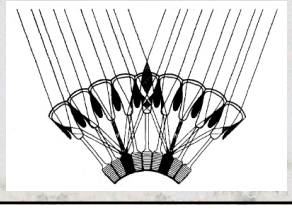


Refracting superposition:
- 'Two-lens telescope'
- Hexagonal facets, conical lenses
- Moths, beetles, some crustaceans, e.g. euphausiid shrimps (krill)

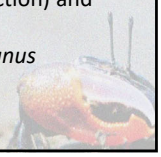




Reflecting superposition:
- Square facets
- Plane mirror in square mirror boxes
- Decapod crustaceans, e.g. shrimps, lobsters and crayfish

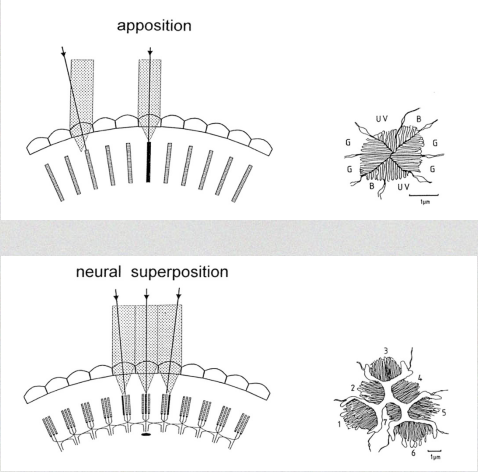


Parabolic superposition:
- Combination of lens (refraction) and curved mirror (reflection)
- Swimming crabs, e.g. *Portunus*



26

Neural superposition eye



- Optically an apposition eye
- Rhabdomeres separated by pigment (cf. normal apposition eye)
- Uses neural connections to enhance sensitivity
- Rhabdomeres in adjacent ommatidia observing same region of space are connected to each other in the lamina
- Increases sensitivity without affecting resolution

27

Compound eyes vs single lens eyes

Advantages:

- Wide and flexible field of view projected onto small sheet of receptors
- Large depth of focus - sensitive to movement at any distance
- Short pathlength of light through the ommatidia reduces loss of UV radiation - allows wide spectral range for vision
- Spherical and chromatic aberration negligible due to short focal length
- Polarisation vision

Disadvantages:

- Diffraction by small lens facets limit resolution
- Small aperture/lenses limit sensitivity

28